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Lodgepole pine forest age class dynamics and susceptibility to mountain pine beetle attack

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Abstract

Because mountain pine beetle attack mature pine stands, an understanding of forest age class dynamics is important to managing forests within the distribution of the beetle. The assumed theoretical negative exponential forest age distribution provides an estimate when ecosystem dynamics are in equilibrium. This study investigates the dynamics of forest age distribution for non-equilibrium ecosystem dynamics, which result primarily from large and irregular stand-replacement fire disturbances that alter the forest age distribution. A model experiment using the SEM-LAND model on a 1 million ha lodgepole pine forest landscape was conducted to estimate how the proportion of susceptible area could be influenced by different fire regimes. The results of the simulation suggest that the temporal dynamics of the area susceptible to mountain pine beetle attack are complex and depend on the fire history of the study area, if the area is experiencing large and irregular stand-replacement fires. The age range of the lodgepole pine forest stands susceptible to mountain pine beetle attack might significantly affect the estimate of the area susceptible to attack.
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1. Introduction

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) is the most destructive insect of mature pine forests in western North America (Wood, 1963). Lodgepole pine (*Pinus contorta* var. *latifolia* Douglis) is the main host species of the MPB in western Canada. In central interior BC, the area infested by the MPB has been increasing since 1995, significantly affecting the timber supply (British Columbia Ministry of Forests, 2003). MPB infestations could also alter other non-timber values of pine forest landscapes, such as wildlife habitat and landscape aesthetics (McDougal, 1975). Determining the extent of the pine forests that are susceptible to MPB attack, therefore, is one of the central issues in

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timber supply prediction and decision making in MPB management.

Lodgepole pine, one of the most widespread tree species in western North America, is distributed from New Mexico to the southern Yukon (Pfister and Daubenmire, 1975). The species is characterized by rapid regeneration and low shade tolerance. Young pine trees grow quickly, while older trees grow more slowly. The species can adapt to various environmental conditions and can therefore grow on most forest sites. The trees can generate cones from young ages. Trees produce both serotinous and non-serotinous cones: the former require temperatures over about 60 °C to release the seeds; thus the species is well adapted to environments with frequent fires. Pine forest landscapes are complex ecosystems and their dynamics depend on a number of environmental conditions, as well as natural disturbances such as MPB, fire, and dwarf mistletoe infestation. Of these disturbances, forest fire can alter the age structure immediately due to its stand-replacement effect.

During outbreaks or epidemics, MPB infests pine forests with a mass attack strategy, and whether a pine tree will die due to the MPB attack is determined by the interaction between the number of MPB individuals attacking a tree and the level of tree resistance (Safranyik, pers. comm., 2003). The level of resistance of a pine stand is related to stand age as wells as stand density and site conditions; resistance increases up to 60 years and then declines (Safranyik et al., 1975). Thus, the susceptibility of a pine stand to MPB attack increases as the stand approaches 60–80 years old, and more mature pine stands will be destroyed by MPB than younger stands. Consequently, the proportion of the pine forest area susceptible to MPB attack will be determined mainly by the stand age distribution across the region under investigation, within climatically suitable conditions.

From a perspective of equilibrium ecosystem dynamics, Van Wagner (1978) proposed a theory that under ideal conditions, forest age follows a negative exponential probability distribution. Taylor and Carroll (2004) applied Van Wagner's model to demonstrate that where forest fire is the primary disturbance agent, forest susceptibility to MPB increases with fire cycle length to a maximum of 25% at 120 years where susceptibility is limited to stands of 80–160 years.

The predicted equilibrium age distribution, however, is not always consistent with observations because the forest is not infinite in size and variation is introduced by the ratio of fire/landscape size (for a given landscape, e.g., this ratio is presented as the percentage of area burned). For example, statistics from forest inventory data indicate that the forest age distribution might not always be negative exponential (e.g., Gray, 1995; Ontario Ministry of Natural Resources, 1996; Carleton, 2000). From an ecological modeling perspective, Armstrong (1999) estimated the mean annual burn rates in a stochastic environment and found that no equilibrium forest age structure could be identified from his simulation results. He thus questioned the validity of equilibrium forest age distribution models and the analysis that relies on these models where the annual burn rate is highly variable. Li and Barclay (2001) investigated the issue with four different models and demonstrated that a stable forest age distribution such as the negative exponential could be expected as long as the forest age-specific mortality is constant over time. However, the stability of forest age distribution will be reduced when a small variation in the age-specific mortality is introduced. Li and Barclay's simulation results suggested that a stable forest age distribution might never be achieved if the forest landscape is subjected to large and irregular stand-replacing disturbances like fire, relative to the landscape size.

Annual burn rates are reported to be high and irregular in Canadian forests (Amiro et al., 2002). However, the burn rates have been declining in lodgepole pine forest in BC for about 80 years (Taylor and Carroll, 2004). In western Canada, forest fires often cause stand-replacement in the burned forest areas, thus altering the forest age distribution. Consequently, the area of the pine forest area that is susceptible to MPB attack could be estimated from the fire regimes of the regions under investigation.

2. Methods

In this paper, we estimate the percentage of the pine forest area that is susceptible to MPB attack under various fire regimes and age susceptibility constraints under non-equilibrium conditions through a model experiment. The model experiment was carried out using a Spatially Explicit Model for LANdscape Dynamics (SEM-LAND) (Li, 2000; Li and Barclay, 2001).

To estimate the area of pine forest susceptible to MPB attack under different fire regimes, we used the SEM-LAND model to simulate the complex interactions among forest growth, fire events, site conditions, landscape structure, and weather conditions.

2.1. The SEM-LAND model

The SEM-LAND model is a landscape fire regime model that simulates long-term dynamics of a forest landscape subject to fire disturbance regimes, operating at 1 ha spatial resolution and yearly time step. Since the model has been documented in Li (2000), only a brief summary will be presented here.

A forest landscape is simulated as a grid of rectangular cells, each cell representing a forest stand with homogeneous site condition, vegetation cover type, and tree age. The model has three main components: forest growth, fire, and regrowth after fire. Forest growth without disturbance is described by standard forest growth equations for Alberta, Canada (Alberta Forest Service, 1984).

A fire event is simulated in two stages: initiation and spread (Li and Apps, 1995, 1996). The fire initiation stage begins with fire ignition and continues until most trees in the 1 ha cell are killed. Whether most trees in the stand would be burned is determined by the fire initiation probability, which is a function of fuel and weather conditions. Once most trees are burned, the fire has the potential to spread to surrounding cells. Whether a neighboring cell would be burned is determined by the fire spread probability, which is a function of not only fuel and weather conditions, but also topographic slope. The simulation of a fire process was driven by the relationships summarized in the Canadian Forest Weather Index (FWI) system (Van Wagner, 1987) and the Canadian Forest Fire Behavior Prediction (FBP) system (Forestry Canada Fire Danger Group, 1992). These relationships characterize how weather conditions will influence fuel moisture, and how fuel moisture and wind speed will affect the rate of fire spread. Based on an assumption that fire initiation and spread probabilities are proportional to the rate of fire spread, the relationships were used in the SEM-LAND model to simulate a detailed fire spread process at the landscape scale. Detailed formulae and equations can be found in Van Wagner (1987), Forestry Canada Fire Danger Group (1992), Hirsch (1996), and Li (2000).

A stand-replacement effect was assumed for the burned area, that is, forest stands are reset to zero if they are burned, or age by 1 year if they are not burned.

2.2. Model experiment

A model experiment was conducted based on a hypothetical lodgepole pine forest landscape of 1 million ha (1000 × 1000 pixels). A coarsely clumped initial forest stand age map was created by randomly assigning an age ranging from 1 to 100 years to each 50 × 50 pixel area (Cary et al., in press). The site index was fixed as 20 m in each of the pixels. A flat terrain was assumed for the landscape in the simulations. Eight fire cycles were originally designed for the simulation experiments: 35, 70, 140, 180, 250, 500, 1000, and 2000 years, through the manipulation of fire probability function shapes. Twelve hundred years simulation was carried out for each run, but in the analysis, we used only results of the last 1000 years to eliminate the effect of initial conditions. Due to the stochastic characteristics of the simulation runs, the final fire cycles were 34, 76, 132, 171, 253, 480, 1082, and 2270 years. The SEM-LAND model was written in FORTRAN 77 and the model simulation experiment was run on a SunBlade 1000 workstation. The CPU time required to complete each simulation varied from a few hours (the longest fire cycle) to about 3 weeks (the shortest fire cycle).

The simulation results were used to calculate the percentage of the three age range groups (80–160 years, 80–250 years, and older than 80 years) at the end of each simulation year. The age ranges were selected because of uncertainties involved in the age of pine forests susceptible to MPB attack. For example, early research suggested that the level of the lodgepole pine tree resistance to MPB attack increases with age up to 60 years, and then declines with increasing tree age (Safranyik et al., 1975). However, under epidemic conditions the size of the beetle population may overwhelm any older-age constraints. Despite of general consensus on lower end of susceptible age around 80 years old, there are diverse perceptions on the upper end of susceptible age ranging from 160 years to unlimited old growth. The three age range groups are designed to catch up with this uncertainty. An average value from the 1000 estimates for each

simulation was used as the estimate of the percentage of the pine forest area susceptible to MPB attack under a specific fire regime.

3. Results

3.1. Temporal dynamics of the area susceptible to MPB attack

Fig. 1 shows the proportion of area susceptible to MPB attack over time in three age range groups. When the fire cycle is short (e.g., 34 years), there is little difference between the groups because frequent large fires keep most forest stands at the young stage and the area susceptible to MPB attack is low for all age groups. With increasing length of fire cycle, the average area burned annually was reduced, resulting in increased chance for the pine stands to become old. Therefore, the percentage of area susceptible to MPB attack will be a function of fire history, that is, large fires reset the forest age in large areas to zero, reducing the area susceptible to MPB attack. When the fire cycle is long (e.g., 2270 years), most forest stands will

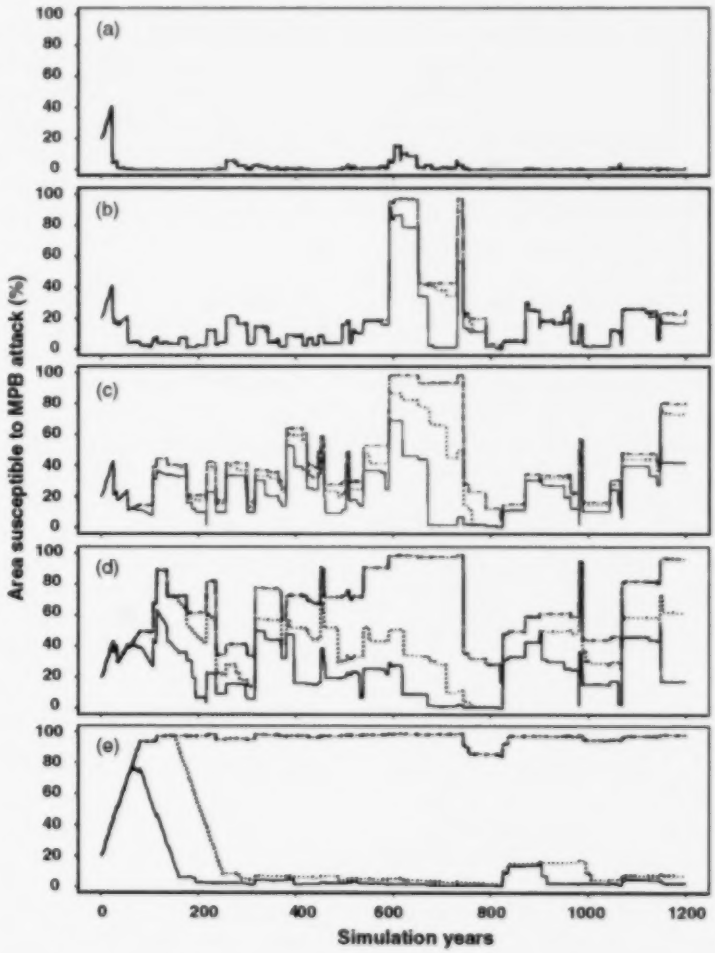

Fig. 1. Simulated percentage of area susceptible to MPB attack under fire cycles of: (a) 34 years, (b) 75 years, (c) 132 years, (d) 253 years, and (e) 2270 years, for three age range groups: 80–160 years (solid lines); 80–250 years (small dotted lines); and older than 80 years (large dotted lines).

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become old, resulting in a small area susceptible to MPB attack based on age ranges of 80–160 and 80–250 years old, and a larger area susceptible to MPB attack in the group of older than 80 years.

3.2. Changing percentage of area susceptible to MPB attack with fire cycles

Fig. 2 shows that if old pine stands escape the MPB attack (age range groups 80–160 and 80–250 years), the area susceptible to MPB attack could first increase with the length of fire cycle as was demonstrated by Taylor and Carroll (2004) for equilibrium conditions, reaching a peak at about 250 years, and then decline gradually with increasing length of the fire cycle. If the old pine stands cannot escape MPB attack, however, the area susceptible to MPB attack could increase with the length of fire cycle, despite this relationship may becomes less ecologically meaningful for fire cycles longer than 500 years, which is about the maximum age of lodgepole pine.

3.3. Variation associated with the 1000 years' changing susceptible percentage

Fig. 3 shows the variability of the area susceptible to MPB attack in the 1000-year simulation. For the group older than 80 years, variation will be highest when the fire cycle is about 140–180 years, but will decline quickly with increasing length of the fire cycle. When the pine stands have a chance to escape MPB attack, the variation associated with different fire cycles could change; the susceptible age range group

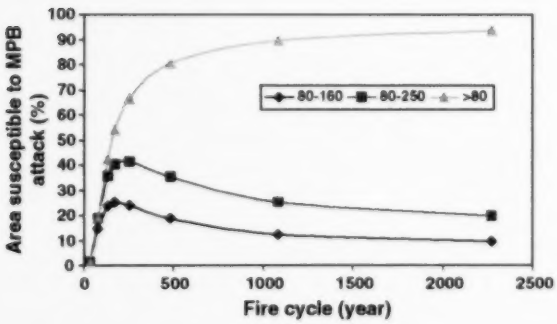

Fig. 2. Area susceptible to MPB attack under various fire cycles for the three age range groups.

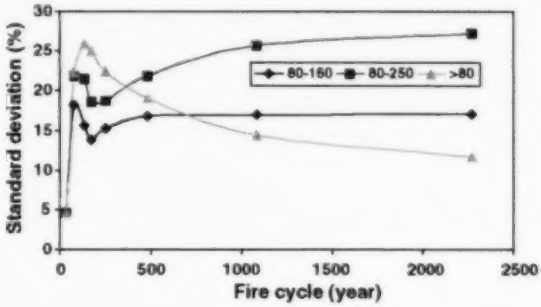

Fig. 3. Standard deviation associated with the estimate of area susceptible to MPB attack under various fire cycles for the three age range groups.

80–250 years could have a higher variation than that in the 80–160 years group.

4. Discussion

The interactions that result in observed patterns are complex in the lodgepole pine forested landscapes. Physical site conditions—including elevation, aspect, slope, soil properties, and weather variables—will influence the growth rate of pine trees, as well as the frequency of natural disturbances. The interactions between fire and MPB disturbance regimes via the dynamics of forest age distribution presented in this paper are a template of the lodgepole pine forest landscape dynamics, which could provide a good example for the study of ecological complexity. The spatially explicit SEM-LAND model simulations presented in this paper demonstrated that the concept of interactions among complex ecosystem components could guide ecological modeling practice to generate information required by management.

4.1. The emergent property and modeling approach

One research focus in the field of ecological complexity is to explore the emergent properties of ecosystem dynamics. Emergent properties are the result of interactions among ecosystem components through non-linear relationships and adaptive capabilities with each other, if any. Also included are the non-equilibrium processes operating far from equili-

brium in open systems, as demonstrated in the studies of self-organization and synergetics (Prigogine, 1980; Haken, 1983). Emergent properties are often studied through mathematical analysis and simulation modeling exercises with examples taken from various disciplines (Bossomaier and Green, 2000).

For studying the complex dynamics and emergent properties of the lodgepole pine forest landscape under various disturbance regimes, ecological modeling appears to be a valid approach for integrating and assimilating known relationships and processes. Each approach has advantages and disadvantages, so that its suitability depends on the questions addressed. In process-based spatially explicit models, a challenge is incorporating the interactions among necessary ecosystem components while conducting the simulations within a reasonable time; faster computers in the future may resolve the computing power requirement. This challenge can be met by identifying the major state variables, processes, components, and relationships that are essential to the exploration of emergent properties. Development of the SEM-LAND model was based on this principle.

4.2. Management applications of the model experiment results

Van Wagner's (1978) theory predicting a constant negative exponential forest age distribution implies that forest landscape dynamics are in equilibrium and thus the area susceptible to MPB attack is more or less stable over time. The simulated dynamic area susceptible to MPB attack (Figs. 1 and 2) can be seen as an emergent property of the hypothetical lodgepole pine landscape, and can provide additional estimates of the area under different fire regimes. These estimates can serve as scenarios under conditions of non-equilibrium ecosystem dynamics. To provide more specific estimates for particular study areas, current lodgepole pine forest landscape conditions are needed as input to the SEM-LAND model to simulate landscape conditions into the future. This will be one of the next steps in our research and will be discussed elsewhere. The effect of non-stand-replacement disturbances on fire risk, such as uneven tree mortality across the landscape due to various spatial distributions in fire intensities and post-beetle forest conditions, will also be addressed elsewhere.

Current simulation results suggest that a more accurate determination of the range of pine stand age susceptible to MPB attack could be an important aspect of a MPB field monitoring program because the age range could affect the estimate of the area susceptible to MPB attack. For example, if old lodgepole pine forest stands are more resistant to MPB attack, the strategy of increasing the effort in fire management could help reduce the amount of susceptible area (Fig. 2). However, if old lodgepole pine forest stands cannot escape MPB attack, increasing effort in fire management could also increase the amount of area susceptible to MPB attack.

From a conceptual perspective, forest resource management, fire management, and pest management on the same forest landscape should be integrated because of the complex dynamics of the lodgepole pine forest landscapes where each management implementation strategy could affect the others. For instance, an increase in fire management effort might reduce the number of fires and the total area burned, allowing forests to grow and increase the timber supply availability. However, fuel might accumulate in the protected areas, increasing the amount of heat released in a future fire, should it occur, making it difficult to contain. From the forest resource management perspective, ideal future forest conditions that sustain maximum forest productivity could be determined from the expected mean forest age and thus a fire management target could be established (Li et al., 2005). That is, unlimited increase in efforts in fire management might not be a good strategy for timber supply. Furthermore, an increase of effort in fire management could also affect the area susceptible to MPB attack, as described above.

4.3. Future research recommendations

Our results suggest that the age range of the pine tree susceptible to MPB attack significantly influences the prediction of the amount of the pine forest susceptible to the MPB attack. This knowledge therefore needs to be strengthened.

Conceptually, the probability of MPB-induced mortality should be the result of interactions among tree resistance, total number of beetles available for attack, and characteristics of the beetle's host selection. The first two components have been

extensively reported in the literature. The effect of phloem thickness and tree age on host selection has also been investigated, however, few reports mention the detail of the beetle's host selection from a behavioral perspective, a factor that might be critical for understanding interactions among the three components. The beetle's host selection may be determined by at least three factors: nutrient contents; thickness of the bark and phloem, which changes with tree age and size; and host phytochemistry, which may be related to drought stress or ability to produce resin a "pitch out" beetle.

Very little is known about fire behavior characteristics in MPB-killed pine stands and thus the effect of MPB on fire probability.

These interactions indicate another dimension of ecological complexity associated with pine forest landscape dynamics. This recommended research would also provide a link between patterns of individual beetle behavior and MPB population dynamics—thus a risk assessment of the pine forest landscape.

5. Conclusions

Temporal dynamics of the area susceptible to MPB attack are complex and depend on the fire history of the study area, if large and irregular stand-replacement fires occur relative to the size of the area, the range of ages of the lodgepole pine stands susceptible to MPB attack could significantly influence the estimate of the area susceptible to MPB attack.

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